

ETHOLOGY OF *EFFERIA CRESSONI* WITH A REVIEW OF THE  
COMPARATIVE ETHOLOGY OF THE GENUS  
(DIPTERA: ASILIDAE)<sup>1</sup>

D. S. DENNIS,<sup>2</sup> R. J. LAVIGNE AND S. W. BULLINGTON<sup>3</sup>

Entomology Section, University of Wyoming, P.O. Box 3354, University Station, Laramie, Wyoming 82071.

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*Abstract.*—The behavior of *Efferia cressoni* (Hine) has been studied in Wyoming, U.S.A. and Mexico. This species exhibited similar behavior patterns in its widely separated habitats except for prey selection (type and size), presence or absence of male searching flights for receptive females with which to mate and daily rhythm of activity. All species of *Efferia*, for which detailed information is available, show similar behavior patterns with respect to foraging and feeding (foraging sites, prey capture methods, immobilization of prey, prey manipulation methods, and prey specificity), male courtship behavior (searching flights) and copulatory position (male over female). Differences in behavior among species of *Efferia* are primarily those of behavior during copulation, duration of copulation and oviposition site chosen. The latter is dependent on the shape of the female's ovipositor.

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The genus *Efferia* is one of the largest among the Asilidae in the United States and Mexico comprising approximately 200 species (Martin, 1965; Martin and Papavero, 1970; Wilcox, 1966). However, behavioral data has been recorded for only 18 species. Some of this information is sketchy and provides limited data on prey specificity and/or foraging sites.

This paper summarizes the available data on this genus (Table 1) and presents information on the ethology of *E. cressoni* (Hine) near Guernsey, Wyoming, U.S.A. and Rancho Experimental "La Campana," Mexico (80 km north of Chihuahua). To our knowledge, this is the first time that behavioral observations have been made on a robber fly species in such widely separated habitats. The almost identical behavior for *E. cressoni* in the two habitats lends support to using behavioral observations as a taxonomic tool.

COMPARATIVE ETHOLOGY OF *EFFERIA CRESSONI*  
IN WYOMING, U.S.A. AND MEXICO

*Methods.*—Methods for gathering and analyzing ethological data for *E. cressoni* in Wyoming were essentially the same as those described for *Neoitamus vittipes*

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<sup>2</sup> Present address: 5875 E. Weaver Circle, Englewood, CO 80111.

<sup>3</sup> Present address: 2139 Catlett Drive, Salem, VA 24153.

(Macquart) in Lavigne (1982). Voucher specimens, on which *E. cressoni* behavioral observations are based, have been placed in the entomological collection of the National Museum of Natural History, Washington, D.C., as lot #52.

Behavioral observations on *E. cressoni* in Wyoming were carried out in Guernsey State Park between June 7 and 20, 1978. The robber fly population inhabited a rocky hillside (Fig. 1) and adjacent gully just west of Guernsey Reservoir. The study area vegetation is typical of that found on the high plains. Common plants included the grasses, *Bouteloua gracilis* (H.B.K.) Lag. ex Steud., *Sitanion hystrix* (Nutt.) J. G. Smith, *Stipa comata* Trin. Rupr., and the forbs, *Allium textile* Nels and Macbr., *Arenaria* sp., *Astragalus missouriensis* Nutt., *Artemisia frigida* Willd., *Gaura coccinea* Nutt. ex Pursh, *Lygodesmia juncea* (Pursh) D. Don, *Opuntia polyacantha* Haw., *Petalostemon candidus* (Willd.) Michx., *Sphaeralcea coccinea* (Pursh) Rhdb., *Tradescantia occidentalis* (Brit.) Smyth, and *Yucca glauca* Nutt.

Behavioral observations on *E. cressoni* in Mexico were reported in Lavigne and Dennis (1985). This species' habitat in Mexico was oak brush savannah in foothills below the Ponderosa Pine zone.

Distribution.—*Efferia cressoni* has not previously been reported as occurring north of Ft. Collins, Colorado. According to Wilcox (1966), this species occurs in Arizona, Colorado, New Mexico and Texas. Both Hine (1919) and Wilcox provided drawings of the superior (upper) forceps which is typically notched at the apex. Wilcox illustrates the lower forceps of the male genitalia with a dorsal, medial "thumb-like" projection or tooth. The male specimens from both Wyoming and Rancho Experimental "La Campana" have a more squared lower forceps and lack the medial projection. However, the ventral fringe of hairs resembles that illustrated by Wilcox.

Foraging and feeding behavior.—*Efferia cressoni* in both Wyoming and Mexico forage from soil, rocks and vegetation (Table 1), depending on the substrate surface temperature. At both locations this species foraged from the ground until the surface temperature reached 40 to 41°C and then they moved onto vegetation. In Mexico, *E. cressoni* forages from vegetation at heights ranging from 5 to 20 cm above the ground, whereas in Wyoming foraging occurred primarily at heights of 7.5 to 12.5 cm. Once *E. cressoni* moved to vegetation, they generally foraged from shaded areas. However, this behavior was not observed as frequently in Wyoming.

*Efferia cressoni* captured prey in flight at distances of 1 m or less. In Wyoming this species was observed to immobilize prey in flight. Immobilization of prey by *E. cressoni* in Mexico has not been observed.

During feeding *E. cressoni* hovered and manipulated prey with all six tarsi prior to reinserting its hypopharynx. At the completion of feeding, prey were pushed off the hypopharynx with the foretarsi while the asilid was still at the feeding site or prey were dropped in flight as the asilid resumed foraging.

The numbers, sizes and percentages of prey of different taxon taken by *E. cressoni* in Wyoming are given in Table 2 and show that Diptera (Fig. 2) constituted 72 percent of the number of prey taken. Lavigne and Dennis (1985) indicate that *E. cressoni* in Mexico fed primarily on Diptera and Homoptera and that these two orders comprised ca. 66 percent of the prey. Presumably differences in prey selection for the two populations are due primarily to availability of prey. As previously indicated, *E. cressoni*'s habitat in Wyoming was near a reservoir and



Figs. 1-2. 1, Rock-studded hillside habitat of *Efferia cressoni* in Guernsey State Park, Guernsey, Wyoming. 2, *Efferia cressoni* male in Wyoming with unidentified Diptera as prey.

this probably contributed to opportunistic predation on Chironomidae which comprise approximately 72 percent of the Diptera prey.

Differences in prey selection between *E. cressoni* in Wyoming (Table 3) and Mexico (Lavigne and Dennis, 1985) are also reflected in the predator to prey ratios. In Wyoming, both sexes fed on smaller prey than was observed for the population in Mexico, as indicated by the larger mean ratio of predator to prey.

Overall *E. cressoni* in Wyoming and Mexico were 3.8 and 2.6 times as large as their prey, respectively. This difference is not surprising since prey size of asilids varies with the taxon of the prey.

The following is a list of prey taken by *E. cressoni* in Wyoming. Lavigne and Dennis (1985) list this species' prey for the population studied in Mexico. COLEOPTERA, Dasytidae: unidentified, VI-11-78 (2 ♀), VI-15-78 (♀), VI-16-78 (4 ♀); Nitidulidae: *Carpophilus pallipennis* (Say), VI-16-78 (♂), VI-18-78 (2 ♂); DIPTERA, Anthomyiidae: unidentified, VI-15-78 (♂); Asilidae: *Efferia cressoni* (Hine), VI-11-78 (♀); *Holopogon seniculus* Loew, VI-16-78 (2 ♀), VI-18-78 (♀); Cecidomyiidae: unidentified, VI-16-78 (♂), VI-18-78 (♀); Chironomidae: unidentified, VI-7-78 (♂), VI-11-78 (7 ♂, 10 ♀), VI-14-78 (2 ♂, 4 ♀), VI-15-78 (♂, 4 ♀), VI-16-78 (5 ♂, 27 ♀), VI-18-78 (2 ♂, 10 ♀); Chloropidae: *Hippelates* sp. prob. *pusio* Loew, VI-16-78 (♀); *Meromyza* sp., VI-18-78 (♀); Phoridae: unidentified, VI-16-78 (♀); Pipunculidae: unidentified, VI-16-78 (♂, ♀); Sciaridae: unidentified, VI-16-78 (2 ♀), VI-18-78 (2 ♀); Simuliidae: unidentified, VI-16-78 (2 ♀), VI-18-78 (♀); Tachinidae: unidentified, VI-7-78 (♀), VI-15-78 (♂, ♀), VI-16-78 (2 ♀); unidentified, VI-16-78 (3 ♀), VI-18-78 (♀); HEMIPTERA, Lygaeidae: *Nysius* sp., VI-14-78 (♀); Miridae: unidentified, VI-15-78 (♂), VI-16-78 (♂, 2 ♀); HOMOPTERA, Aphididae: unidentified winged adult, VI-14-78 (♀); Cicadellidae: *Aceratagallia* sp., VI-14-78 (♀); *Aceratagallia uhleri* (Van Duzee), VI-14-78 (♂); *Athysanella* sp., VI-16-78 (♀); *Cuerna* sp., VI-14-78 (♀), VI-15-78 (♀); *Flexamia flexulosa* (Ball), VI-11-78 (♀), VI-14-78 (♀); *Flexamia* sp., VI-16-78 (♀); unidentified, VI-11-78 (♀), VI-14-78 (2 ♀); nymph, VI-15-78 (♂), VI-16-78 (♀), VI-18-78 (♀); Issidae: *Bruchomorpha beameri* Doering, VI-14-78 (♀); HYMENOPTERA, Ichneumonidae: Chalcidoidea, VI-15-78 (♀), VI-16-78 (♂, 3 ♀); LEPIDOPTERA, unidentified: VI-11-78 (♀), VI-14-78 (♀), VI-15-78 (♀); ORTHOPTERA, unidentified: nymph, VI-11-78 (♀).

In both Wyoming and Mexico *E. cressoni* exhibited cannibalism. In Wyoming, this species also was observed two times to be preyed on by jumping spiders (Salticidae). One of the spiders was identified as *Pellenes* sp., *viridis* group.

Mating behavior. — Male *Efferia cressoni* in Mexico have been observed making searching flights for receptive females with which to mate. However, this behavior was not observed in Wyoming.

Matings were initiated in flight when the male grasped the female on the dorsum of her thorax and the struggling pair fell to the ground. The male then clasped the female's genitalia and the pair typically flew onto vegetation.

During mating *E. cressoni* remain in the male-over-female position (Fig. 3). In this position the male's abdomen curved around to the right or left of the female's abdomen and clasped her genitalia from below. The male's and female's wings were generally spread at a 30 to 45 degree angle to their bodies (some males folded their wings over their dorsum). *Efferia cressoni* males in Mexico rested their foretarsi on the female's eyes; males in Wyoming also rested their foretarsi on the dorsum of the female's thorax.

In Mexico, two complete matings for this species were 7 and 7.5 min. Partial copulation times for *E. cressoni* in Wyoming ranged from 1 to 10 min., but only one complete mating was observed to last 5.5 min. As mating neared completion, males frequently briefly buzzed their wings. Then, just before termination, males buzzed their wings again, moved to the female's side and pushed off with all six

Table 1. Comparative ethology of eighteen species of *Efferia*.<sup>1</sup>

	<i>E. aestuans</i>	<i>E. albi-barbis</i>	<i>E. argyro-gaster</i>	<i>E. benedicti</i>	<i>E. bicau-data</i>	<i>E. cressoni</i> (Mex)	<i>E. cressoni</i> (Wyo)	<i>E. frewingi</i>
Foraging Sites								
From soil	X		X	X	X	X	X	X
From vegetation	X		X	X	X	X	X	X
Prey Capture Methods								
On soil								X
On vegetation								
In air			X	X	X	X	X	X
Immobilization of Prey								
In air			X	X	X	X	X	X
At feeding site								X
Prey Manipulation Methods								
Hovers in air—all legs			X	X	X	X	X	X
On soil—crawls on prey								
On soil—combination of legs								
Prey Specificity								
Stenophagic							X	
Euryphagic	X	X	X	X		X		X
Cannibalism Observed								
				X		X	X	X
Courtship Behavior of Males								
None observed			X				X	
Searching flights				X		X		X
Buzzes wings in flight								
Copulatory Position								
Male over female			X	X	X	X	X	X
Behavior During Copulation								
Pair quiet unless disturbed								
Male intermittent wing buzz						X	X	X
Male terminal wing buzz			X			X	X	X
Male strokes female's abdomen			X					X
Male moves female's head with foretarsi				X				
Pair moves from ground to vegetation			X					X
Male falls off to side at termination of mating						X	X	
Duration of Copulations								
Range in minutes			6-7.5			7-7.5		6-24
Average in minutes			6.75	1.75		7.25	5.5	14.9

Table 1. Extended.

<i>E. helenae</i>	<i>E. interrupta</i>	<i>E. kondratieffi</i>	<i>E. nemoralis</i>	<i>E. pallidula</i>	<i>E. pogonias</i>	<i>E. rapax</i>	<i>E. staminea</i>	<i>E. subcuprea</i>	<i>E. triton</i>	<i>E. varipes</i>
X				X	X		X	X	X	X
X		X	X	X	X		X	X	X	X
									X	X
X				X			X	X	X	X
X				X			X	X	X	X
X				X				X	X	X
X	X			X		X	X	X	X	X
X		X		X			X			
X				X			X		X	X
									X	
X				X			X	X	X	X
X				X						
	X									
X								X	X	
							X			
										X
								X	X	
4-12				1.5			3	6.5	0.75-1.5	11.5-14
7.6								6.5	1.0	12.76

Table 1. Continued.<sup>1</sup>

	<i>E. aestuans</i>	<i>E. albibarbis</i>	<i>E. argyro-gaster</i>	<i>E. benedicti</i>	<i>E. bicau-data</i>	<i>E. cressoni</i> (Mex)	<i>E. cressoni</i> (Wyo)	<i>E. frewingi</i>
Oviposition Sites								
In or on vegetation	X		X	X		X	X	
In soil		?						X
Duration of Ovipositions								
Range in minutes			0.5–1.5	2.5–3		0.75–1.0		0.9–2
Average in minutes						0.88		1.7
Number of Eggs/Clutch	1–90		2–19			2–5		3–7
Average Egg Measurements (mm)								
Length	0.8		1.2			1.41		1.63
Width	0.25		0.4			0.54		0.72

<sup>1</sup> The behavioral data for the genus is compiled from the authors' observations and the following published sources: Baker and Fischer, 1975 [*E. aestuans* (Linnaeus)]; Bromley, 1914 [*E. aestuans*, *E. rapax* (Osten Sacken)], 1930 [*E. interrupta* (Macquart), *E. rapax*], 1942 [*E. aestuans*], 1945 [*E. aestuans*, *E. albibarbis* (Macquart), *E. interrupta*, *E. rapax*], 1946a [*E. aestuans*, *E. interrupta*, *E. rapax*], 1946b [*E. aestuans*, *E. rapax*], 1948a [*E. aestuans*], 1948b [*E. aestuans*, *E. albibarbis*, *E. rapax*], 1950 [*E. aestuans*, *E. albibarbis*, *E. interrupta*, *E. rapax*]; Bullington and Lavigne, 1984 [*E. kondratieffi* Bullington and Lavigne]; Dennis and Lavigne, 1976, [*E. varipes* (Williston)]; Fattig, 1945 [*E. aestuans*, *E. albibarbis*, *E. femorata* (Macquart), *E. rapax*]; Hull, 1942 [*E. interrupta*]; Lavigne, 1964 [*E. helenae* (Bromley)], 1972 [*E. bicaudata* (Hine), *E. helenae*], 1979 [*E. argyrogaster* (Macquart)]; Lavigne and Dennis, 1975 [*E. frewingi* Wilcox], 1985 [*E. cressoni* (Hine), *E. subcuprea* (Schaeffer), *E. triton* (Osten Sacken)]; Lavigne et al., 1976 [*E. benedicti* (Bromley)], 1980 [*E. frewingi*]; Lavigne and Holland, 1969 [*E. helenae*, *E. pallidula* (Hine), *E. staminea* (Williston)]; Lavigne and Pfadt, 1966 [*E. bicaudata*, *E. helenae*, *E. pallidula*, *E. staminea*]; Linsley, 1960 [*E. interrupta*, *E. rapax*]; McAtee and Banks, 1920 [*E. aestuans*, *E. albibarbis*, *E. nemoralis* (Hine)]; Painter, 1926 [*E. albibarbis*]; Reinhard, 1938 [*E. aestuans*]; Rogers and Lavigne, 1972 [*E. bicaudata*, *E. helenae*, *E. pallidula*, *E. staminea*, *E. varipes*]; Scarbrough, 1972 [*E. aestuans*, *E. interrupta*], 1974 [*E. aestuans*, *E. pogonias* (Wiedemann)].

legs (Fig. 4). Some male *E. cressoni* in Wyoming also have been observed to vigorously pump their genitalia up and down towards the end of mating. This behavior was not reported by Lavigne and Dennis (1985) for males in Mexico.

Temperatures at the heights (5 cm to 1 m above the ground) of copulating pairs of *E. cressoni* on vegetation ranged from 25–40°C in Wyoming; those in Mexico were 27.2 and 29.4°C.

Oviposition behavior.—Female *E. cressoni* oviposited in grass seed heads, and between the sheath and stem of grass stalks (Fig. 5). Temperatures taken at heights (10–12 cm) of *E. cressoni* ovipositions in Wyoming ranged from 29.4–37.8°C, those in Mexico at 33–34°C.

Eggs have not been collected for *E. cressoni* in Wyoming, but in Mexico females deposited 2 to 5 eggs per oviposition. These eggs had an average length and width of 1.41 and 0.54 mm, respectively.

Daily rhythm of activity.—A comparison of the daily rhythm of activity of *E. cressoni* in Wyoming and at Rancho Experimental "La Campana," shows that at the latter site this species exhibited more distinct, shorter periods of mating and oviposition behavior throughout the day. In Wyoming, *E. cressoni* had less distinct, longer periods of mating, oviposition and foraging behavior (Fig. 6). This relatively constant level of behaviors, may in part be due to the relatively rapid

Table 1. Extended.

<i>E. helenae</i>	<i>E. inter-rupta</i>	<i>E. kondratieff</i>	<i>E. nemo-ralis</i>	<i>E. pallidula</i>	<i>E. pogo-nias</i>	<i>E. rapax</i>	<i>E. staminea</i>	<i>E. sub-cuprea</i>	<i>E. triton</i>	<i>E. varipes</i>
X	?			X X		?	X	?	X	X
0.5-1.5									0.6-2	0.5-3
0.75									1.23	1.75
1-7				1-15			2-10		3-13	10-40
1.31				1.09			1.30		1.72	1.28
0.48				0.41			0.36		0.58	0.41

changing weather in Wyoming during the summer and the need by flies to take advantage of good weather.

#### COMPARATIVE ETHOLOGY OF *EFFERIA*

Foraging and feeding behavior.—All species of *Efferia* studied to date forage from both the ground (soil, rocks, twigs, etc.) and vegetation, depending on the soil surface temperature. Foraging from the ground takes place until the surface temperature reaches 40 to 49°C. Above this range of temperatures, *Efferia* move onto vegetation to forage. One species, *E. subcuprea*, forages primarily from vegetation at heights of 1 to 2 m and rarely ventures to the ground. *Efferia aestuans* also forage mainly from vegetation and only occasionally from the ground.

*Efferia* exhibit other adaptations to temperature fluctuations. During cooler parts of the day they frequently flatten themselves against the ground, with their bodies broadside to the sun. When ground temperatures approach the point where the asilids begin to move onto vegetation, they assume various postures, such as holding their bodies high off the substrate and facing the sun. Additionally, *E. triton* has been observed to hold its foretarsi over its head at high ground temperatures. While on vegetation *Efferia* frequently move into the shade of rocks and vegetation. Similar adjustments to temperature have been observed for other species of Asilidae. These adjustments allow the robber flies to function in areas of optimal temperature.

As *Efferia* forage, they often face into the sun, thus backlighting potential prey objects and presumably making them more easily discerned. In addition, some species (e.g. *E. varipes*) rest with their bodies at a 40 to 45 degree angle to the substrate. Since the central ommatidia of an asilid's eye have greater powers of vision than do the outer ones (Melin, 1923), this posture probably also allows the asilids to see prey more clearly. As they rest at ground level or on vegetation, *Efferia* move their heads more frequently than their bodies.

*Efferia* often chase potential prey or make investigatory flights while foraging. They also capture and release potential prey if they cannot insert their hypopharynx or find the prey unsuitable because of some other characteristics.



Table 2. Numbers and percentages of prey of different taxa captured by males and females of *Efferia cressoni* in Wyoming.

Taxa	Males				Females			
	No.	%	Range (mm)	$\bar{x}$	No.	%	Range (mm)	$\bar{x}$
Coleoptera	1	3.6	3.2	3.2	9	7.8	2.8-3.6	3.2
Diptera	22	78.6	1.6-5.7	3.6	81	70.4	1.0-13.5	3.1
Hemiptera	2	7.1	2.1-2.8	2.5	3	2.6	2.7-6.5	4.2
Homoptera	2	7.1	2.5-3.4	3.0	14	12.2	2.3-8.0	4.5
Hymenoptera	1	3.6	2.6	2.6	4	3.5	0.8-2.7	1.5
Lepidoptera	—	—	—	—	3	2.6	5.9-6.5	6.2
Orthoptera	—	—	—	—	1	0.9	0.9	0.9
Total	28	100	1.6-5.7	3.5	115	100	0.8-13.5	3.3

While the forage flights of most *Efferia* cover distances up to 5 m, prey are usually captured within 1 to 2 m of a foraging site. *Efferia triton* is the only species which has been observed to capture prey at the same mean distances it forages. Lavigne and Dennis (1985) suggest that this species may have better vision than other *Efferia* species.

Prey are usually captured in the air. However, three species (*E. frewingi*, *E. triton* and *E. varipes*) have been reported occasionally to capture prey on soil or vegetation.

Once prey are captured *Efferia* usually insert the hypopharynx into the prey prior to landing to feed, often times while hovering above the site. Additionally, *Efferia frewingi* and *E. subcuprea* occasionally immobilize prey on the ground, presumably because of the prey's large size or because of the difficulty encountered in subduing the prey.

During feeding the most common method of repositioning prey prior to reinserting the hypopharynx, is hovering above the feeding site and manipulating the prey with all six tarsi. *Efferia subcuprea*, *E. triton* and *E. varipes* also manipulate prey with a combination of legs while resting on the soil, and *E. varipes* may crawl over its prey before reinserting its hypopharynx. These latter two methods appear to be utilized when the prey is too large to be manipulated during a hover flight. Other members of the subfamily Asilinae to which *Efferia* belongs, also commonly hover while manipulating prey.

Upon completion of feeding prey are usually, (1) pushed off the asilid's hypopharynx with the foretarsomeres while the asilid is still on the feeding site, or (2) dropped in flight as the asilid moves to a new location and/or resumes foraging.

With the exception of *E. varipes* and *E. cressoni* in Wyoming, the *Efferia* studied

Table 3. Comparison between length of *Efferia cressoni* and that of its prey in Wyoming.

Sex	Predator Length (mm)*			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Minimum	Maximum	Mean	Minimum	Maximum	Mean		
Male	10.5	14.0	12.3	1.6	5.7	3.5	28	3.5
Female	11.3	16.0	13.6	0.8	13.5	3.3	115	4.1
Species Mean			12.9			3.4		3.8

\* 10 predators of each sex were measured.



Figs. 3-4. 3, *Efferia cressoni* pair in copula on plant stem in Wyoming. 4, *Efferia cressoni* male in first phase of separation from female in Wyoming.

to date appear to be fairly non-selective in their choice of prey (i.e. euryphagic—no one insect order makes up more than 50 percent of the prey). In the case of *E. varipes*, Orthoptera made up 52 percent of its prey (Dennis and Lavigne, 1976), while Diptera served as 72 percent of the prey of *E. cressoni* in Wyoming. For several other species, one or two orders (usually Diptera, Homoptera and/or Hymenoptera) may represent 30 to 40 percent of the prey taken.

Cannibalism is practiced by most *Efferia* species. Members of the genus can serve as prey for other species of Asilidae, including other *Efferia*. As previously



Fig. 5. *Efferia cressoni* female ovipositing in Wyoming.

indicated, jumping spiders (Salticidae) have been observed preying on *E. cressoni* in Wyoming. Mites also have been observed attached to various parts of bodies of *E. frewingi*.

**Mating behavior.**—Prior to the initiation of mating, most *Efferia* males, for which there is adequate data, exhibit searching flights for receptive females. These flights usually consist of males weaving in-and-out of vegetation looking for females. Additionally, *E. triton* males buzz their wings during these flights, thus providing a possible auditory stimulus.

Most matings are initiated in flight when the male overtakes the female and the struggling pair falls to the ground where mating ensues in the male-over-female position. *Efferia benedicti*, *E. helenae*, *E. staminea* are the only species which have been observed to initiate mating on the ground or vegetation.

While in the male-over-female position, the male's abdomen curves around to the right or left of the female's abdomen and clasps her genitalia from below. The male's and female's wings are generally spread at a 30 to 45 degree angle to their bodies, although some males may fold their wings over their bodies. The male's foretarsi typically rest on the female's eyes.

During copulation some *Efferia* (e.g. *E. cressoni*) move from the soil surface to vegetation. Males of most species studied exhibited wing buzzing during mating (especially a terminal buzz) or stimulatory behavior using the fore or hind tarsi. When these behaviors occur towards the end of copulation, they may also signal to the female that the end of mating is imminent. As previously indicated, some male *E. cressoni* in Wyoming also have been observed to vigorously pump their genitalia up and down towards the end of mating.

Most *Efferia* mate for about 6 to 14 min. *Efferia bicaudata*, *E. pallidula*, *E. staminea* and *E. triton* mate for less than 3 min.; whereas, *E. frewingi* may mate for as long as 24 min.

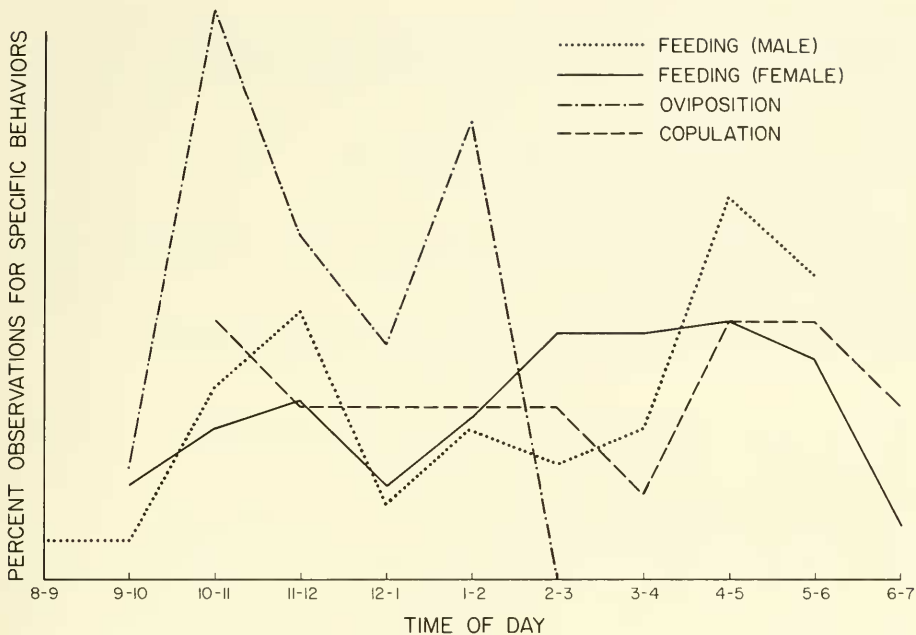


Fig. 6. The diurnal rhythm of activity of *Efferia cressoni* in Wyoming. (The percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations of each behavior—45, 146, 20, 15—for male feeding, female feeding, mating and oviposition, respectively.)

*Efferia* typically terminate mating when the male does one or more of the following, (1) falls to one side of the female and pushes off using all tarsomeres (e.g. *E. cressoni*, Fig. 4), (2) crawls up on the female's dorsum and pushes off, (3) rises into the air and flutters his wings while releasing his claspers (only *E. benedicti*), and (4) pushes off of the female without falling to one side, crawling up on the female's dorsum or rising into the air.

Oviposition behavior.—The site of egg deposition depends primarily on the shape of the female's ovipositor. Females with cylindrical ovipositors (i.e. *E. frewingi* and *E. helenae*) deposit eggs in the soil, while females with laterally flattened ovipositors deposit eggs in or on vegetation (e.g. *E. cressoni* in Wyoming). *Efferia pallidula* is the only species that has been observed to oviposit in both soil and vegetation; its ovipositor is laterally flattened.

Individual ovipositions take from 0.5 to 3 min., during which generally 2 to 19 eggs are laid. *Efferia varipes* and *E. aestuans* are the only species reported to deposit more than 19 eggs/clutch. For those species which can be followed by the investigator for extended periods of time, multiple ovipositions can usually be observed.

All collected *Efferia* eggs are oval-oblong and creamy-white. Average widths range from 0.25 to 0.72 mm; average lengths range from 0.8 to 1.72 mm.

Daily rhythm of activity.—Some detailed information on daily activity pattern has been reported for five species of *Efferia*: *cressoni*, *subcuprea*, and *triton* in Mexico (Lavigne and Dennis, 1985), and *frewingi* (Lavigne and Dennis, 1975) and *varipes* (Dennis and Lavigne, 1976) in Wyoming. That of *E. cressoni* in

Wyoming was discussed previously in this paper. All six of these species forage throughout the day with one or two peak periods of activity. These peaks are often slightly more pronounced than the remaining time periods. However, mating and/or oviposition behavior are generally restricted to one or two time periods of the day. For example, in Wyoming the majority of ovipositions by *E. cressoni* females takes place between 1000 and 1500 h (Fig. 6).

As the percentage of asilids engaged in one particular behavior increases, the percentage engaged in other behaviors decreases (e.g. in Wyoming female *E. cressoni* foraging activity is least during the midday period and greatest during late afternoon from 1500 to 1700 h). Additionally, temperature may be important in determining the occurrence of different behaviors throughout the day.

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